

GALL FORMATION BY THE CAPITULUM-INFESTING FRUIT FLY,
TEPHRITIS STIGMATICA (DIPTERA: TEPHRITIDAE)

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Abstract.—Known heretofore only as a capitulum-infesting species, *Tephritis stigmatica* (Coquillett) also is reported here to develop in galls formed on branches and stems of *Senecio douglasii* (deCandolle) (Asteraceae) in southern California. Two generations of galls occur each year on *S. douglasii*, with immature larvae in juvenile, F₂ galls constituting at least part of the overwintering population. One or more larvae feed gregariously in interconnected, central longitudinal, short-branched feeding tunnels in the expanded pith. As many as six individuals, including five puparia, were found in one F₂ gall. Florets (including ovaries) were fed upon in ungalled capitula and F₁ and F₂ galls were formed on branches and stems of *S. douglasii* at some locations, but gall-formation is the much less common and less widespread mode of development. Galls are described and pictured.

Tephritis stigmatica (Coquillett) is the only tephritid among the 17 species in this genus currently described from North America north of Mexico for which the life history and behavior have been reported in any detail (Foote 1960a, Tauber and Toschi 1965, Foote and Blanc 1979). Tauber and Toschi (1965) studied this species reared from capitula of *Senecio integerrimus* Nuttall (Asteraceae), a common perennial shrub in central- and northeastern-montane California (Munz and Keck 1959, Munz 1968). In 1981, I first reared what appeared to be *T. stigmatica* or an undescribed congener from galls on branches and stems of *Senecio douglasii* (deCandolle), another common perennial shrub in the same genus, but widely distributed below ca. 1500 m in California (Munz and Keck 1959, Munz 1968). The capitula of *S. douglasii* also are widely infested by *T. stigmatica* (Foote and Blanc 1963, Tauber and Toschi 1965, Wasbauer 1972).

Tephritis dilacerata Loew is fairly well known from studies by Berube (1978) and

Shorthouse (1980), but this European species is an obligate gall former in capitula and stems of its host, unlike the unique host-plant relationship reported herein. Several other species of *Tephritis* are known to form capitulum and stem galls; others to infest capitula without forming galls, but none to do both (Freidberg 1984). The purpose of this report is to describe gall formation by *T. stigmatica* as a unique alternative mode of development for this tephritid heretofore known only from capitula.

MATERIALS AND METHODS

Galls on branches and stems of *S. douglasii* from which adults recently had emerged and galls containing larvae or puparia were sampled at two locations in southern California south of Lamont Peak at Spanish Needle Creek, Sequoia Nat. Forest, Kern Co., on 24 VII 1984, 7 VIII 1984, and 3 III 1987; and 2 km south of Pearblossom, San Bernardino Co., on 22 IV 1985 and 12 II 1987.

Fully-grown larvae and puparia extracted

from some of these galls were placed individually in glass shell vials with perforated plastic caps and held for adult emergence at room temperature in a covered bell jar at near-saturation R.H. The external morphology of adults reared from these and several other collections of galls were compared at magnifications of up to $50\times$ to *T. stigmatica* adults reared from capitula of *S. douglasii* and other Asteraceae sampled throughout southern and central California during 1980–86.

All host-plant identifications were made by or confirmed by A. C. Saunders, Curator of the Herbarium of the University of California, Riverside. The plant nomenclature used is that of Munz and Keck (1959) and Munz (1968, 1974); the insect nomenclature, that of Foote (1959, 1960a).

RESULTS

Taxonomy.—The 26 ♂ and 32 ♀ reared from puparia dissected from branch and stem galls (18 ♂ and 29 ♀ were reared from the first Pearblossom sample) showed no consistent differences compared to adults of *T. stigmatica* reared from capitula. The larvae feed on the florets (including ovaries) but do not gall the capitula of *S. douglasii* (personal observation). Other than body size, body parts examined, measurements taken, and ratios calculated in this study (Table 1) were the same as those used by Quisenberry (1951) of Nearctic *Tephritis*, including *T. stigmatica*, and by Foote (1959) in his diagnosis of the most recently described species of *Tephritis*.

Foote and Blane (1963, p. 72) termed *T. stigmatica* "the largest of the California *Tephritis* species." *T. stigmatica* adults reared from branch and stem galls on *S. douglasii* were larger on the average than adults reared from capitula of both *S. douglasii* and *S. integerrimus* (Table 1). The size of adults reared from capitula of these and other Asteraceae also varied considerably (Table 1). This probably reflected the different nutritional value of the capitula of varying size

and maturity (S. N. Thompson, *in litt.* 1987), as well as the degree of larval development when the heads were sampled. A tiny male reared from a capitulum of *Haplopappus venetus* (Humboldt) Blake ssp. *vernonioides* (Nuttall) Hall, an uncommon and apparently nutritionally ill-suited host (as well as a new host genus and species record, Wasbauer 1972) at Cardiff-by-the-Sea, San Diego Co., on 15 × 1980, illustrates the extreme effect of host-plant unsuitability on adult size in *T. stigmatica* (Table 1). Differences in mean head-part measurements as indices of body size differences (Foote 1960a) between males and females and among flies reared from galls versus capitula of the same or different host plants alone were insufficient to warrant description of the gall-forming flies as a separate species. F. L. Blanc, California Department of Food and Agriculture (Retired), Sacramento, confirmed that specimens in Table 1 were *T. stigmatica* (*in litt.* 1987).

Galls.—*Tephritis stigmatica* overwinters in southern California at least partly as immature larvae in F_2 galls formed mostly on low axillary branches on *S. douglasii* (Fig. 1a). Adults that emerge from heads in late summer and fall also overwinter. Young F_2 galls examined in February (mid-winter) in 1987 at Pearblossom and early March 1987 at Spanish Needle Creek were a third to half of full size. Most F_2 galls (Fig. 1b), like ungalled, elongating current season branches, showed darker (purple) coloration than galls and branch growth formed later in the year. The pigmentation could favor solar energy adsorption and facilitate larval and pupal development as well as adult emergence during cooler months of the year. Galls and ungalled branches that develop during the hot summer are mostly light green (Fig. 1a, 1d). As many as five axillary branches bore F_2 galls along one 10-cm basal section of stem (Fig. 1a). In contrast, F_1 galls usually were isolated on upper parts of aerial stems and usually contained only one or two tephritids (Fig. 1d). Dissection of 72 juvenile

Table 1. Mean ($\pm$ SE) and range of size and distance measurements (mm)^a of head parts, and selected ratios thereof ($\bar{x} \pm$ SE)^b of *Tephritus stigmatica* adults reared from galls on *Senecio douglasii* and from capitula of *S. douglasii*, *S. integerrimus*, and *Haplopappus venetus* in California.

Adults Measured		Head		Gena Width		Frons Width		Distance from Vertex to Lunule		Frons Width		Eye Width	
No	Sex	Height		Length		Eye		Height		Eye		Height	
26	♀	1.00 ± 0.01	0.90 ± 0.01	(0.90-1.05)	(0.83-1.00)	0.13 ± 0.00	0.83 ± 0.01	(0.10-0.15)	(0.78-0.93)	0.72 ± 0.01	0.58 ± 0.01	(0.65-0.80)	(0.53-0.65)
		= 1.11 ± 0.01				= 0.16 ± 0.00				= 1.24 ± 0.01			
32	♀	1.01 ± 0.01	0.09 ± 0.01	(0.85-1.10)	(0.88-1.13)	0.14 ± 0.01	0.87 ± 0.01	(0.13-0.15)	(0.73-0.95)	0.76 ± 0.01	0.60 ± 0.01	(0.68-0.98)	(0.53-0.65)
		= 1.07 ± 0.01				= 0.16 ± 0.00				= 1.29 ± 0.03			
5	♂	0.91 ± 0.01	0.82 ± 0.01	(0.88-0.95)	(0.80-0.85)	0.12 ± 0.02	0.76 ± 0.01	(0.10-0.13)	(0.75-0.80)	0.60 ± 0.01	0.50 ± 0.03	(0.55-0.63)	(0.48-0.53)
5	♀ ^d	= 1.14 ± 0.01				= 0.15 ± 0.01				= 1.21 ± 0.02			
5	♂	0.91 ± 0.03	0.81 ± 0.02	(0.80-1.00)	(0.70-0.88)	0.12 ± 0.01	0.74 ± 0.01	(0.10-0.15)	(0.68-0.80)	0.62 ± 0.01	0.48 ± 0.02	(0.58-0.70)	(0.43-0.58)
5	♀ ^c	= 1.13 ± 0.01				= 0.16 ± 0.01				= 1.30 ± 0.04			
1	♂ ^e	0.70-0.63				0.10-0.60				0.50-0.40			
		= 1.12				= 0.17				= 1.25			

¹⁴ After Ouisenberry (1951) and Foote (1959).

Calculated from individual micrometer measurements.

^a Calculated from individual micrometer measurements.

Reared from *S. douglanissi* flower heads collected at Cañon Junction, San Bernardino Co., 8 VII 1981.

Reared from *S. douglasii* flower heads collected at Cajon Junction, San Bernardino Co., in 1967.
Reared from *S. mutanarinus* flower heads collected at Jackass Meadow, Sequoia Nat. Forest, Tulare Co., 20 VI 1986.

^eReared from *S. integriramus* flower heads collected at Jackass Meadow, Sequoia Nat. Forest, Inyo Co., 20 VI 1980.
^fReared from *Haplophragma venetus* ssp. *vernomooides* flower heads collected at Cardiff-by-the-Sea, San Diego Co., 15 X 1980.

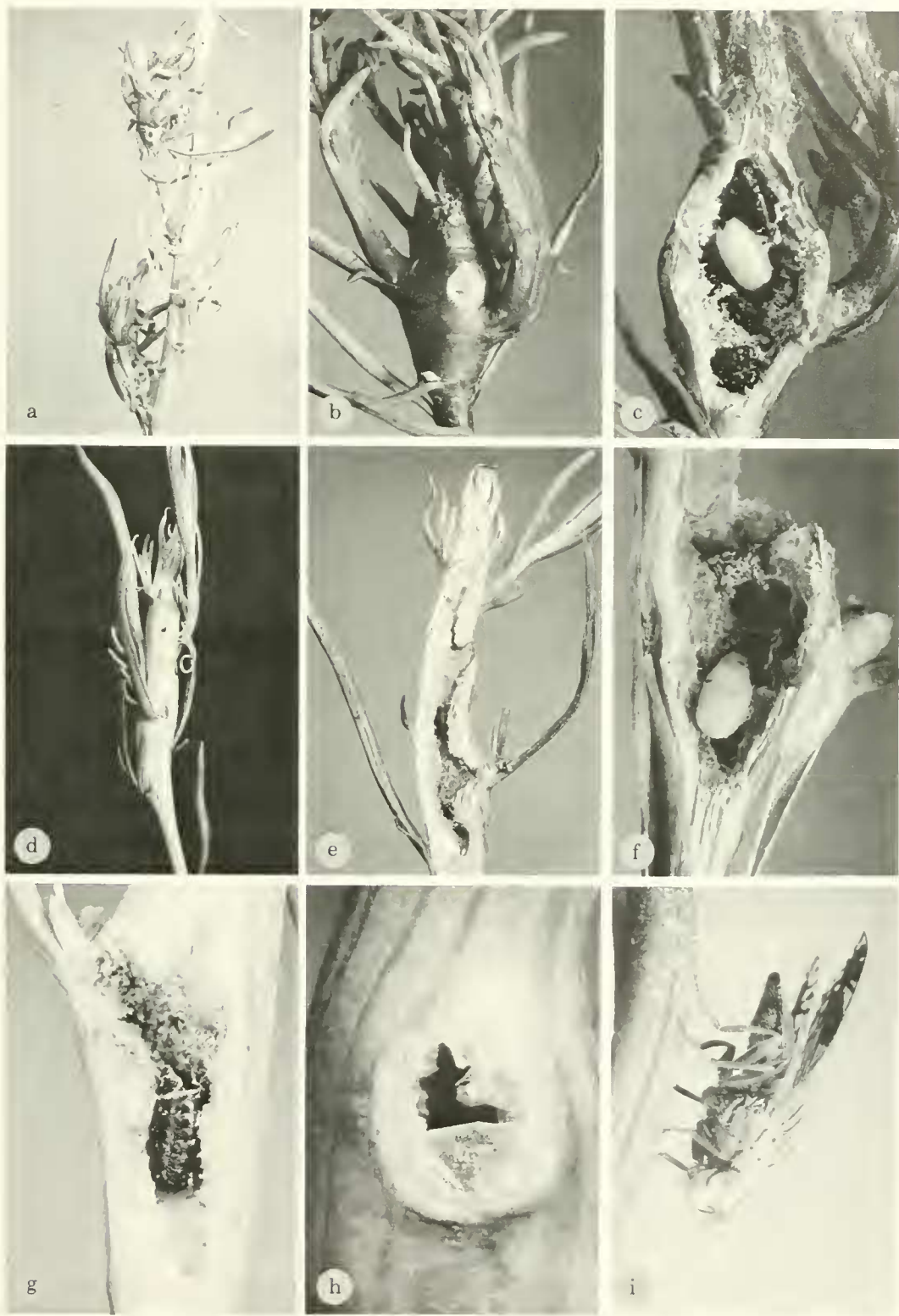
overwintering F_2 galls yielded mostly 2nd instars and small to half-grown 3rd instars. A few fully-grown larvae and puparia also were found in F_2 galls collected in early March at Spanish Needle Creek. From one to five individuals in the same or different stages of growth, e.g. 2nd instars and puparia, were found together in overwintering F_2 galls within interconnected, longitudinal, short-branched feeding tunnels.

Fifty overwintered, fully-formed F_2 galls collected at Pearblossom in April, 1985, contained an average of 1.5 (range, 1–6) fully-grown larvae and intact or empty puparia (Fig. 1c). All but one of the 50 galls were spindle-shaped (Fig. 1b, 1d). These galls either were sessile or born on pedicels of various lengths, up to 5 mm long. These F_2 galls tapered apically as a result of continued apical meristem growth and branch elongation distal to the gall; whereas, death of the apical meristem from larval feeding resulted in a club-shaped gall, or curved gall as a lateral branch assumed apical dominance (Goeden and Ricker 1981, Goeden 1987). Dissections suggested that multiple ovipositions by one or more F_1 females in an axillary bud initiated the formation of a F_2 gall during the previous fall; whereas, a female emerging from these galls the following spring probably oviposited in the apical meristem of an upright aerial stem to initiate F_1 galls. Capitula production was observed to be delayed on F_1 gall-bearing plants sampled at Spanish Needle Creek in early August, 1984.

Branch and stem galls are formed from expanded pith tissue, the branches and stems swelling to about three times normal di-

ameter (Fig. 1b, 1d). Vascular strands were deflected outward and followed the gall contour. Irregular masses of hypertrophied parenchyma cells lined the walls of the feeding chamber(s), resembling round, shiny globules which the larvae scored with mouthhooks while feeding. Frass lined the feeding tunnels of the late-stage 3rd instars (Fig. 1c, 1g). Only part of the gall mass was consumed by a single larva (Fig. 1e, 1g); although, the interiors of smaller galls, especially those containing two or more larvae, were largely consumed (Fig. 1b). Forty-two, spindle-shaped, overwintered, fully formed F_2 galls collected at Pearblossom in 1985 averaged 2.4 ± 0.1 (range, 1.4–3.2) cm in length and 6.5 ± 0.2 (range, 4–10) mm in greatest diameter. These galls incorporated as many as six nodes as indicated by the number of lateral branches arising thereon. The fully-grown larva extends its feeding tunnel distally and outward to, but not through, the epidermis leaving a round, thin, 2-mm dia., translucent window to the outside through which the emerging adult eventually exits (Fig. 1f, 1h, 1i). Once the window is formed, the larva returns to its feeding tunnel and pupariates, often with the anterior part of the puparium projecting into the exit tunnel, and usually facing the window (Fig. 1g). The larval predecessor of one of 75 (1.3%) puparia examined in overwintered Pearblossom galls tunneled basally in constructing its exit tunnel. A maximum of three windows was formed in one gall from Pearblossom that contained five puparia and one larva; otherwise, most galls contained a single window through which as many as three flies emerged. Exit holes

Fig. 1. Galls of *Tephritis stigmatica* on *Senecio douglasii*: a, overwintering, juvenile, axillary-branch, F_2 galls ($0.8\times$); b, fully-formed, dark-pigmented, spindle-shaped, F_2 gall with lateral window ($2.1\times$); c, same gall as in b opened to expose four puparia within ($3.3\times$); d, fully-formed, compound, F_1 gall showing lateral exit hole ($0.8\times$); e, same gall as in d opened to expose two empty puparia in interconnected, central-longitudinal feeding tunnel and two lateral exit tunnels ($1.3\times$); f, fully-grown larva just having completed an exit tunnel ending in circular window ($4.5\times$); g, puparium at juncture of short feeding tunnel and lateral exit tunnel ($4.6\times$); h, closeup view of broken, epidermal window on gall surface ($3.6\times$); i, newly-emerged female reared from gall ($7.6\times$).



usually were constructed in the distal third or half of the overwintered Pearblossom galls at, below, or between the nodes (Fig. 1b, 1d, 1e, 1f, 1g, 1h). Either one or both sexes of flies (Fig. 1i) emerged from individual F_2 galls.

Among 39 F_1 galls collected at Spanish Needle Creek, only one (2.8%) was club-shaped, and the remainder, spindle-shaped. The 32 spindle-shaped F_1 galls from which flies had emerged in the field in the fall were 4.7 ± 0.3 cm (range, 2.0–7.5) long and 8 ± 1 (range, 5–10) mm wide at their widest. These spindle-shaped galls incorporated an average of 4 (range, 1–8) nodes. The 39 F_1 galls contained one or two, empty, or intact and parasitized, puparia in interconnected central-longitudinal feeding tunnels (Fig. 1e). Thirty-three of these galls had contained a single tephritid and six had contained two tephritids (Fig. 1e), which as noted above was considerably less than the number of individuals in F_2 galls from Pearblossom (Fig. 1c). The feeding tunnels in these F_1 galls averaged 1.3 ± 0.2 (range, 0.5–3.5) cm in length and were 2 mm wide. The exit tunnels averaged 3 (range, 2–5) mm in length and also were circular and 2 mm in cross-sectional width. Ten intact and mostly parasitized empty puparia in these galls averaged 4.2 ± 0.1 (range, 3.6–4.6) mm in length and 1.9 ± 0.0 (range, 1.7–2.0) mm in width. An unidentified species of *Eurytoma* (Hymenoptera: Eurytomidae) was reared from these puparia.

Galls were collected from *S. douglasii* at the following locations in addition to those noted above: 2 ♂ reared from galls collected south of Hesperia at Mojave River Forks, San Bernardino Nat. Forest, San Bernardino Co., on 21 IV 1981; 8 ♂ reared from galls collected at Orcutt, Santa Barbara Co., on 23 VI 1981; 1 ♂ and 1 ♀ reared from galls collected at Cajon Junction, San Bernardino Co., on 8 VII 1981. This represents only a small fraction of uncounted demes of *S. douglasii* examined, but found to lack galls during my many wide-ranging field trips

throughout southern California during 1981–1986.

DISCUSSION

Morphological study of *T. stigmatica* from galls and capitula on *S. douglasii* to date has failed to support what otherwise might have been interpreted as sympatric speciation occurring on the same species of host plant. For example, Goeden (1987) reported that the somewhat rare native tephritid, *Tripanea conjuncta* (Adams), facultatively either galls the apical meristems or develops gregariously feeding on florets (including ovaries) in capitula of its sole host plant, *Trixis californica* Kellogg (Asteraceae). This was the first published report of this facultative mode of development in nonfrugivorous Tephritidae (Zwölfer 1983, Freidberg 1984, Price et al. 1986). However, with *T. stigmatica*, a member of the genus most closely allied to *Tripanea* according to Foote (1959, 1960a, 1960b), development in capitula or galls apparently are not mutually exclusive activities on *S. douglasii* at a particular site and season, i.e. both gall formation and feeding in capitula may occur simultaneously during summer into fall. However, gall formation apparently is the requisite mode of development for the F_1 generation on *S. douglasii* earlier in the year. And, I suspect that at least part of the overwintered generation produced in branch (axillary bud) galls begun during the preceding year, as well as overwintered adults produced in *S. douglasii* capitula, reproduce in summer at higher elevations in capitula of a succession of alternate hosts, e.g. *S. integerrimus* and *S. triangularis* Hooker (Wasbauer 1972), on which galls apparently are not formed (Tauber and Toschi 1965). This part of the life history of *T. stigmatica* needs clarification.

Individual host plants were observed at Spanish Needle Creek on March 3, 1987, that bore current and previous year's F_2 galls as well as F_1 galls on dead upright stems that terminated on branches with last year's ca-

pitula containing empty puparia. This provided evidence of three successive generations reproducing as gall formers augmented by a capitula-infesting generation on the same host individuals commensurate with the seasonal development described above.

As previously noted, galls have not been found on *S. douglasii* at most locations where and when plants were examined in the field as opportunity allowed since 1981, indicating the absence of some unknown environmental requisite(s) for gall formation by *T. stigmatica*. This spotty incidence of a gall-forming insect occupying only tiny, discrete, often distant, fractions of the total geographic range of its native host plant also was documented for the stem-galling moth, *Carollela beevorana* Comstock (Lepidoptera: Cochylidae) by Goeden and Ricker (1981). In contrast, a congener of *C. beevorana* commonly forms galls on a related host plant throughout a large part of southern California (Goeden and Ricker 1986).

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